

ceae has been discussed (Fallen, 1986; Kunze, 1990; Nilsson et al., 1993; Judd et al., 1994; Sennblad & Bremer, 1996; Endress & Bruyns, 2000).

The pollinarium (Bookman, 1981) of most Asclepiadaceae is composed of two or more *pollinia*, each of which contains all of the microspores of a single anther locule embedded in a hard matrix, and a *translator* apparatus, which develops from a stigmatic secretion and mechanically attaches the pollinia to a pollinator (Corry, 1883; Frye, 1902; Safwat, 1962; Schill & Jäkel, 1978; Kunze, 1993; Swarupanandan et al., 1996). Pollinarium structure has been the most important and consistently used character for the delimitation of major groups (subfamilies and tribes) of Asclepiadaceae (Brown, 1811; Endlicher, 1838; Decaisne, 1844; Schumann, 1895; Rosatti, 1989; Swarupanandan et al., 1996; Civeyrel et al., 1998). Studies of the development and mature structure of pollinaria have been carried out by Corry (1883), Frye (1902), Safwat (1962), Schill and Jäkel (1978), Kunze (1993), Civeyrel (1994), and Verhoeven and Venter (1997, 1998a, b, 2001 this volume). The evolution of the structure of pollinaria has been discussed by Safwat (1962), Wanntorp (1988), Kunze (1993, 1995a), Judd et al. (1994), Sennblad and Bremer (1996), Swarupanandan et al. (1996), and Civeyrel et al. (1998).

The gynostegium is composed of the postgenitally united stamens and carpels of the flower. The five stamens are typically connate throughout their length and joined by their anthers to the apex of the united styles. However, the filaments are free in Periplocoideae (Judd et al., 1994; Swarupanandan et al., 1996). Except for Periplocoideae, the encircling anthers completely block access to the stigmatic regions, except for narrow slits through which pollinia must enter to effect pollination (Kunze, 1991). Thus, pollinaria and gynostegia each exhibit a high degree of synorganization between androecium and gynoecium, with regard to both structure and function (Corry, 1883; Fallen, 1986; Endress, 1994). The evolution of the gynostegium has been well studied, particularly with respect to intermediate forms present in related Apocynaceae (Fallen, 1986; see also Wanntorp, 1988; Judd et al., 1994).

The corona is composed of one or more whorls of structures attached to, or located between, the corolla and androecium. Coronas are exceedingly diverse in Asclepiadaceae; they may be expressed as rings, scales, pads, or cups, often with several highly elaborated components present in the same flower (Kunze, 1990, 1995b, 1997; Liede & Kunze,

1993). Coronas have been the subject of structural and developmental studies (e.g., Frye, 1902; Hofmann & Specht, 1986; Kunze, 1990, 1995b, 1997; reviewed in Endress, 1994), and hypotheses of homology and transformation among corona types have been presented (Kunze, 1990; Liede & Kunze, 1993). Coronas have also been studied with respect to their functions in pollination (Wanntorp, 1974; Kunze, 1991, 1997; Endress, 1994). These functions include providing optical cues to pollinators (Endress, 1994), guiding insects into the proper position for pollinia removal and insertion by mechanically positioning proboscides (Kunze, 1991) or legs (Fishbein & Venable, 1996), and producing, conveying, and storing nectar (Galil & Zeroni, 1965; Kunze, 1990, 1997). However, the evolution of these structures has not been studied in an explicitly phylogenetic context.

Analysis of the evolution of corona morphology is hampered by uncertainty regarding the homology of corona structure and position across Asclepiadaceae. Although coronas have been the subject of intensive study, the conflicting interpretations of previous workers are surely the result of the exceptional diversity of forms and the seemingly fluid association of coronas with corolla and androecium in closely related taxa (e.g., Schumann, 1895; Woodson, 1941; Good, 1956; Hofmann & Specht, 1986; Kunze, 1990; Liede & Kunze, 1993; Nilsson et al., 1993). Liede and Kunze (1993; see also Kunze, 1990), echoing Woodson's (1941) and Good's (1956) attempts to bring consistency to the descriptions of coronas across Asclepiadaceae, concisely reviewed the uncertainties and discrepancies of past treatments and presented a typological framework for corona description. In addition, they presented a hypothetical transformation series linking their four basic corona types (Liede & Kunze, 1993, Fig. 1). In their descriptive system, a fundamental distinction was drawn between coronas of corolline derivation ("corolline" and "annular" types) and staminal derivation ("staminal" and "interstaminal" types). This distinction was previously emphasized by Good (1956). Kunze (1995b) emended this system by recognizing the dorsal anther appendages of some Gonolobinae as a fifth type of corona. The transformation series presented by Liede and Kunze (1993) implicitly assumed homology among their corona types, yet their discussion of particular coronas explicitly rejected the homology of different types. As recognized by Kunze (1990; Liede & Kunze, 1993), developmental studies would provide crucial data for homology assessment (Kaplan, 1984).

Phylogenetic and ontogenetic studies are required to more robustly assess the homology among the various structures termed “corona” in Asclepiadaceae (cf. Hufford, 1996a, b). In this paper, I analyze the evolution of the corolline, staminal, and interstaminal types, in order to focus on the origin and early diversification of coronas in Asclepiadaceae. For convenience, I group staminal and interstaminal coronas (Liede & Kunze, 1993) into “gynostegial” coronas, in order to emphasize and explore the homology between coronas that appear to be of staminal and corolline derivation (Schumann, 1895; Good, 1956; Kunze, 1990). Of the corona types of Liede and Kunze (1993; Kunze, 1990, 1995b), annular and dorsal coronas are of restricted distribution among apparently derived taxa (especially genera nested within Gonolobinae and Ceropogoniae) and are not considered here.

I use a preliminary phylogenetic hypothesis for Asclepiadaceae to investigate the origin and diversification of pollinaria and coronas. The evolution of the gynostegium was achieved in large part in apocynaceous ancestors of Asclepiadaceae (Fallen, 1986) and will not be addressed here. For pollinaria and coronas I ask the following questions about the evolution of these structures: (1) Where in the phylogenetic history of Asclepiadaceae did pollinaria and coronas originate? (2) What are the patterns of diversification and homoplasy in pollinaria and coronas? and (3) What are the sensitivities of evolutionary reconstructions to uncertainties about homology and phylogenetic accuracy?

MATERIALS AND METHODS

Structural data were gleaned from the literature and based to a lesser extent on my own observations. Character states were coded for exemplar taxa sampled for a preliminary phylogenetic analysis (Tables 1, 2; L. Civeyrel & M. Fishbein, unpublished data). Thorough study of character states present in larger clades was used to assess whether the coding of exemplars accurately reflected ancestral states of larger clades. The coding of coronal characters owes much to the careful observations of Kunze (1990, 1995b, 1997) and Endress (Nilsson et al., 1993; Endress & Bruyns, 2000), and to the conceptual framework of Liede and Kunze (1993; Kunze, 1990). Characters, their states, and a discussion of character coding are presented in Table 3. The evolution of pollinaria and coronas was analyzed by reconstructing the history of transformations under the criterion of maximum parsimony, as implemented in MacClade, version 3.05 (Maddison & Maddison, 1992).

The phylogenetic hypothesis used for the analysis of floral evolution was derived from published and unpublished analyses of chloroplast *matK* sequences (Civeyrel et al., 1998; Civeyrel & Fishbein, unpublished data). The particular phylogeny on which the analyses were conducted resulted from a preliminary analysis of partial *matK* sequences using maximum parsimony (Fig. 1). Analyses of complete sequences, voucher information, and methodological details will be published elsewhere. Species sampled and the higher taxa to which they belong (after Liede & Albers, 1994; Liede, 1997) are reported in Table 1. Outgroups were chosen from among the closest relatives of Asclepiadaceae in Apocynaceae s.l. (Civeyrel et al., 1998). Sensitivity of reconstructions of character evolution to a specific phylogenetic hypothesis was investigated by examining another published phylogeny based on chloroplast *rbcL* sequence data (Sennblad & Bremer, 1996). Consideration of this hypothesis is important because of the non-monophyly of Asclepiadaceae in the published analysis of *rbcL* sequences (Sennblad & Bremer, 1996; i.e., Periplocoideae are placed in a clade with non-asclepiad Apocynaceae, rather than as sister to Secamonoideae + Asclepiadoideae; see also Potgieter & Albert, 2001 this volume).

RESULTS AND DISCUSSION

ORIGIN AND DIVERSIFICATION OF POLLINIA

The evolution of pollinia in Asclepiadaceae has been relatively conservative with regard to the presence and number of pollinia (Fig. 2). Little homoplasy was required for evolutionary reconstructions based on several schemes of weighting changes among character states (0, 2, or 4 pollinia per stamen). Assuming equal transition probabilities implies one or two origins of pollinia, outside of Periplocoideae. It is equally parsimonious to infer that pollinia originated once in the common ancestor of Asclepiadoideae and Secamonoideae or independently in these subfamilies. Under the former scenario, the ancestral pollinia number could be inferred with equal parsimony to be two or four per stamen, with either a subsequent change to four pollinia in Secamonoideae or two pollinia in Asclepiadoideae, respectively. Under the second scenario, pollinia of Asclepiadoideae and Secamonoideae would be convergent and not phylogenetically homologous (Patterson, 1982). However, the uniqueness of the asclepiad pollinium among angiosperms and the similarity between pollinia of Secamonoideae and Asclepiadoideae (Safwat, 1962; Schill & Jäkel, 1978; Civeyrel, 1994; Civeyrel et al., 1998;

Table 1. Taxa studied and their suprageneric classification (after Liede & Albers, 1994; Liede, 1997; cf. Endress & Bruyns, 2000).

| Species | Subfamily (Tribe; Subtribe) |
|---|--|
| Ingroup | |
| <i>Camptocarpus mauritianus</i> (Lam.) Decne. | Periplocoideae |
| <i>Cryptostegia grandiflora</i> R. Br. | Periplocoideae |
| <i>Hemidesmus indicus</i> (L.) R. Br. ex Schult. | Periplocoideae |
| <i>Periploca graeca</i> L. | Periplocoideae |
| <i>Raphionacme welwitschii</i> Schltr. & Rendle | Periplocoideae |
| <i>Schlechterella abyssinica</i> (Chiov.) Venter & R. L. Verh. ^a | Periplocoideae |
| <i>Pervillaea venenata</i> (Baill.) Klack. | Secamonoideae |
| <i>Secamone bosseri</i> Klack. | Secamonoideae |
| <i>Secamone parvifolia</i> (Oliv.) Bullock | Secamonoideae |
| <i>Secamone volubilis</i> (Lam.) Marais | Secamonoideae |
| <i>Secamonopsis madagascariensis</i> Jum. | Secamonoideae |
| <i>Fockea capensis</i> Endl. | Asclepiadoideae (Fockeeae) |
| <i>Dischidia formosana</i> Maxim. | Asclepiadoideae (Marsdenieae) |
| <i>Dregea sinensis</i> Hemsl. | Asclepiadoideae (Marsdenieae) |
| <i>Marsdenia edulis</i> S. Watson | Asclepiadoideae (Marsdenieae) |
| <i>Marsdenia laxiflora</i> Donn. Sm. | Asclepiadoideae (Marsdenieae) |
| <i>Stephanotis floribunda</i> Brongn. | Asclepiadoideae (Marsdenieae) |
| <i>Frerea indica</i> Dalzell | Asclepiadoideae (Ceropegieae ^b) |
| <i>Huernia</i> cf. <i>thuretii</i> Cels | Asclepiadoideae (Ceropegieae) |
| <i>Riocreuxia burchellii</i> K. Schum. | Asclepiadoideae (Ceropegieae) |
| <i>Asclepias asperula</i> (Decne.) Woodson | Asclepiadoideae (Asclepiadeae; Asclepiadinae) |
| <i>Asclepias subaphylla</i> Woodson | Asclepiadoideae (Asclepiadeae; Asclepiadinae) |
| <i>Asclepias virletii</i> E. Fourn. | Asclepiadoideae (Asclepiadeae; Asclepiadinae) |
| <i>Asclepias zanthodacryon</i> (L. B. Sm.) Woodson | Asclepiadoideae (Asclepiadeae; Asclepiadinae) |
| <i>Pergularia daemia</i> (Forssk.) Chiov. | Asclepiadoideae (Asclepiadeae; Asclepiadinae) |
| <i>Tylophora indica</i> (Burm. f.) Merr. | Asclepiadoideae (Asclepiadeae; Astephaninae ^c) |
| <i>Vincetoxicum nigrum</i> (L.) Moench | Asclepiadoideae (Asclepiadeae; Astephaninae ^c) |
| <i>Gonolobus arizonicus</i> (A. Gray) Woodson | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Gonolobus</i> sp. nov. aff. <i>uniflorus</i> HBK | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Gonolobus xanthotrichus</i> Brandegee | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Matelea</i> sp. nov. aff. <i>parvifolia</i> (Torr.) Woodson | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Matelea quirosii</i> (Standl.) Woodson | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Schubertia grandiflora</i> Mart. & Zucc. | Asclepiadoideae (Asclepiadeae; Gonolobinae) |
| <i>Cynanchum laeve</i> (Michx.) Pers. | Asclepiadoideae (Asclepiadeae; Metastelminae) |
| <i>Cynanchum palmeri</i> (S. Watson) S. F. Blake | Asclepiadoideae (Asclepiadeae; Metastelminae) |
| <i>Cynanchum utahense</i> (Englem.) Woodson | Asclepiadoideae (Asclepiadeae; Metastelminae) |
| <i>Pentarrhinum insipidum</i> E. Mey. | Asclepiadoideae (Asclepiadeae; Metastelminae) |
| <i>Sarcostemma clausum</i> (Jacq.) Schult. | Asclepiadoideae (Asclepiadeae; Metastelminae) |
| <i>Araujia sericifera</i> Brot. | Asclepiadoideae (Asclepiadeae; Oxypetalinae) |
| <i>Morrenia odorata</i> (Hook. & Arn.) Lindl. | Asclepiadoideae (Asclepiadeae; Oxypetalinae) |
| Outgroup | |
| <i>Apocynum androsaemifolium</i> L. | |
| <i>Strophanthus divaricatus</i> (Lour.) Hook. & Arn. | |

^a Reported as *Triodoglossum abyssinicum* (Chiov.) Bullock by Civeyrel et al. (1998); included in *Raphionacme* by Venter and Verhoeven (1997); see Venter and Verhoeven (1998).

^b Ceropegieae Orb. has priority over Stapelieae Decne. and should be adopted as the tribal name (J. Reveal, *Index Nominum Suprageneroricum Plantarum Vascularium*, <<http://matrix.nal.usda.gov:8080/star/supragenericname.html>>, consulted 11 February 2000).

^c Removed from Astephaninae by Liede (2001 this volume).

Table 2. Matrix of character states of pollinia and coronas for the taxa in Table 1. Character names, state names, and discussion of character coding are presented in Table 3.

| Taxon | 1 | 2 | 3a | 3b | 4a | 4b |
|---|---|---|----|----|----|----|
| <i>Camptocarpus</i> | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Cryptostegia</i> | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Hemidesmus</i> | 1 | 0 | 1 | 1 | 0 | 0 |
| <i>Periploca</i> | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Raphionacme</i> | 0 | 0 | 1 | 0 | 0 | 1 |
| <i>Schlechterella</i> | 1 | 0 | 1 | 0 | 0 | 1 |
| <i>Pervillaea</i> | 1 | 2 | 0 | 0 | 1 | 1 |
| <i>Secamone bosseri</i> | 1 | 2 | 0 | 0 | 1 | 1 |
| <i>Secamone parvifolia</i> | 1 | 2 | 1 | 1 | 1 | 1 |
| <i>Secamone volubilis</i> | 1 | 2 | 0 | 0 | 1 | 1 |
| <i>Secamonopsis</i> | 1 | 2 | 1 | 1 | 1 | 1 |
| <i>Fockea</i> | 2 | 2 | 0 | 0 | 2 | 2 |
| <i>Dischidia</i> | 2 | 2 | 0 | 0 | 1 | 1 |
| <i>Dregea</i> | 2 | ? | 0 | 0 | 1 | 1 |
| <i>Marsdenia edulis</i> | 2 | 2 | 0 | 0 | 1 | 1 |
| <i>Marsdenia laxiflora</i> | 2 | 2 | 0 | 0 | 1 | 1 |
| <i>Stephanotis</i> | 2 | 2 | 0 | 0 | 1 | 1 |
| <i>Frerea</i> | 2 | 2 | 0 | 0 | 2 | 2 |
| <i>Huernia</i> | 2 | 2 | 0 | 0 | 2 | 2 |
| <i>Riocreuxia</i> | 2 | 2 | 0 | 0 | 2 | 2 |
| <i>Asclepias asperula</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Asclepias subaphylla</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Asclepias virletii</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Asclepias zanthodacryon</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Pergularia</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Tylophora</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Vincetoxicum</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Gonolobus arizonicus</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Gonolobus</i> sp. nov. aff. <i>uniflorus</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Gonolobus xanthotrichus</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Matelea</i> sp. nov. aff. <i>parvifolia</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Matelea quirosii</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Schubertia</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Cynanchum laeve</i> | 2 | 1 | 0 | 0 | 1 | 1 |
| <i>Cynanchum palmeri</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Cynanchum utahense</i> | 2 | 1 | 0 | 0 | 0 | 0 |
| <i>Pentarrhinum</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Sarcostemma</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Araujia</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Morrenia</i> | 2 | 1 | 0 | 0 | 2 | 2 |
| <i>Apocynum</i> | 0 | 0 | 1 | 1 | 0 | 0 |
| <i>Strophanthus</i> | 0 | 0 | 1 | 1 | 0 | 0 |

at the time of origin. The number of pollinia per stamen is a direct consequence of the number of fertile anther locules (Safwat, 1962; Swarupandan et al., 1996). As in most angiosperms, all Apocynaceae, except Asclepiadoideae, have four-locular anthers. The inference of an ancestral number of two pollinia per stamen would require a less parsimonious reversal from two anther locules to four in Secamonoideae, rather than retention of the ancestral condition. Thus, a single origin of pollinia in the common ancestor of Asclepiadoideae and Secamonoideae, in which four pollinia were produced by four-locular anthers, is strongly favored over alternate hypotheses. According to this scenario, presence of pollinia is a synapomorphy of Asclepiadoideae + Secamonoideae and reduction from four to two pollinia per stamen is a synapomorphy of Asclepiadoideae (Judd et al., 1994). It should also be noted that pollinia of some Secamonoideae may be united, giving the appearance of one or two pollinia per pollinarium, but this condition is clearly derived and secamonoid anthers are invariably four-locular (Civeyrel, 1994; Civeyrel et al., 1998; Endress & Bruyns, 2000).

Pollinia have been reported from as many as seven genera of Periplocoideae (Schill & Jäkel, 1978; Nilsson et al., 1993; Verhoeven & Venter, 1994, 1998a, b, 2001; Venter & Verhoeven, 1997; Endress & Bruyns, 2000), although these have been reduced to six genera in the most recent classification (Venter & Verhoeven, 2001 this volume). The rigorous comparative study of the pollen morphology of asclepiads by Verhoeven and Venter (1998b, 2001) summarizes the salient similarities and differences among pollinia of Periplocoideae, Secamonoideae, and Asclepiadoideae. Pollinia of Periplocoideae and Secamonoideae retain two ancestral features that are modified in most Asclepiadoideae (with the notable exception of *Fockea* Endl.): production of pollen tetrads and the absence of a pollinium wall. However, pollinia of Periplocoideae lack a derived feature common to all examined Secamonoideae and Asclepiadoideae—the reduction of the inner wall layers of pollen tetrads. Among Periplocoideae bearing pollinia, all genera are Asian, except African *Schlechterella* K. Schum. (syn. *Triodoglossum* Bullock), which differs in producing multiporate tetrads (Verhoeven & Venter, 1998a). This difference led Verhoeven and Venter (2001) to predict that the origins of pollinia in Asia and Africa were independent. From the foregoing observations, one may draw the following conclusions regarding the phylogenetic homology of pollinia of asclepiads: (1) pollinia of Asclepiadoideae and Secamono-

Verhoeven & Venter, 2001) suggest that the hypothesis of a single origin of pollinia is to be favored. Any step matrix in which the origin of pollinia is less likely (no matter how slightly) than a change between two and four pollinia per stamen favors a single origin of pollinia.

Consideration of the structure of anthers in Periplocoideae and non-asclepiad Apocynaceae favors the reconstruction of four, rather than two, pollinia

Table 3. Character names, state names, and discussion of character coding. All characters are treated as unordered in evolutionary reconstructions using maximum parsimony. The effect of relaxation of this assumption for character 1 is discussed in the text.

1. Number of pollinia per stamen: none (0), four (1), two (2). Pollen morphology of Asclepiadaceae has been surveyed and summarized by Brown (1811), Corry (1833), Schill and Jäkel (1978), Swarupanandan et al. (1996), Civeyrel (1994; Civeyrel et al., 1998), and Verhoeven and Venter (1998b, 2001). Coding of the number of pollinia is unambiguous for Asclepiadoideae and Secamonoideae. Pollen grains of Periplocoideae are typically shed in tetrads. However, pollinia have been reported (Schill & Jäkel, 1978; Verhoeven & Venter, 1994, 1998a, 1998b, 2001; Venter & Verhoeven, 1997). These pollinia differ from those of Asclepiadoideae and Secamonoideae in their softer consistency and well-developed inner walls of the tetrads (Endress & Bruyns, 2000; Verhoeven & Venter, 2001). However, pollinia of Periplocoideae are similar to those of the Secamonoideae and *Fockea* (Asclepiadoideae) in consisting of tetrads and lacking a distinct pollinium wall (Verhoeven & Venter, 2001). With the limited sampling of Periplocoideae in the present study, pollinia are reconstructed as independently derived in Periplocoideae (in *Hemidesmus* and *Schlechterella*) and remaining Asclepiadaceae. Two origins of pollinia were hypothesized for Periplocoideae by Verhoeven and Venter (2001), with one origin putatively homologous to the pollinia of Secamonoideae and Asclepiadoideae. However, the sparse distribution of genera containing pollinia across the recognized tribes of Periplocoideae (Venter & Verhoeven, 1997) suggests that multiple origins (and perhaps even losses) of pollinia might be inferred. A more refined understanding of the phylogeny of Periplocoideae will undoubtedly yield important insights into the homology and evolution of their pollinia.
2. Position of attachment of translator to pollinia: pollinia absent (0), attachment apical (1), attachment basal (2). Translator attachment of Periplocoideae is coded as absent, because the mechanism in this subfamily is via adhesion, following flower maturation. This condition differs substantially from Secamonoideae and Asclepiadoideae, in which attachment of pollinia to the translator occurs much earlier in development, by a different mechanism (Brown, 1811; Safwat, 1962; Kunze 1993; Swarupanandan et al., 1996). The classic division of Asclepiadoideae into three tribes was based on the orientation of the pollinium relative to the translator: pendent, horizontal, or erect (Brown, 1811; Endlicher, 1838). Subsequently, this division was challenged as artificial due to imprecision in the description of the point of attachment of translators to pollinia (Woodson, 1941; Swarupanandan et al., 1996). I have coded the orientation of the pollinium relative to the translator following Swarupanandan et al. (1996), although their homology criterion has recently come under question (Endress & Bruyns, 2000).
- 3a. Corolline corona: absent (0), present (1). The definition of this character follows the description of Liede and Kunze (1993; see also Kunze, 1990; Nilsson et al., 1993). The primary homology criterion is topological. Corolline coronas are composed of five distinct elements positioned on the corolla, proximal to and radially aligned with the corona sinuses. This definition explicitly excludes annular coronas, which are composed of united segments, or are unsegmented (Woodson, 1941; Good, 1956; Liede & Kunze, 1993). Character state coding differs from that of character 3b only for Periplocoideae. Several genera of this subfamily have contradictory or ambiguous descriptions of the position of corona elements (i.e., corolline vs. gynostegial; Kunze, 1990; Nilsson et al., 1993; Klackenberg, 1998). In coding character 3a, I have assumed that corolline coronas are present in all Periplocoideae that have coronas, following the observations of Kunze (1990) and Klackenberg (1998). Other taxa were coded based upon the observations of Hooker (1883), Woodson (1941), Sundell (1981), Rosatti (1989), Kunze (1990, 1997), Klackenberg (1992a, 1992b, 1995), Li et al. (1995), Civeyrel and Klackenberg (1996), Forster (1996), Liede (1996), and personal observations.
- 3b. Corolline corona: absent (0), present (1). Coding of this character is identical to that in character 3a, except that *Raphionacme*, *Schlechterella*, and *Camptocarpus* are coded as lacking corolline coronas. Coronas in these genera are assumed to be positioned on the gynostegium, as observed by Nilsson et al. (1993) in *Raphionacme*.
- 4a. Gynostegial corona: absent (0), composed of free staminal segments (1), composed of united staminal and inter-staminal segments (2). The definition of this character follows Liede and Kunze (1993; see also Kunze, 1990). Dorsal anther coronas of Gonolobinae (Kunze, 1995b) are specifically excluded. Gynostegial coronas include those coronas that are attached to the staminal column, but not the corolla. In cases where the corona is attached to both the androecium and corolla, a gynostegial corona is coded as present if the attachment to the column is clearly much greater than to the corolla. Ambiguous cases in Periplocoideae are treated with separate codings, as in characters 3a and 3b. In character 4a, all Periplocoideae are coded as lacking gynostegial coronas (cf. character 3a; Kunze, 1990; Klackenberg, 1998). Gynostegial coronas have been subdivided into those composed of five distinct segments aligned radially with the staminal filaments and lacking any discernible union among segments ("staminal") and those composed of segments that are united at least basally, sometimes forming a cylinder around the gynostegium, and often with apically free segments that are in positions both aligned with the filaments and alternating with them ("united staminal and interstaminal"). These latter coronas may achieve a high degree of complexity, appearing to be constructed of multiple whorls of segments (e.g., *Frerea*, *Ceropegieae*). Observations are based on the sources listed in the discussion of character 3a.
- 4b. Gynostegial corona: absent (0), composed of free staminal segments (1), composed of united staminal and inter-staminal segments (2). Coding of this character is identical to that in character 4a, except that *Raphionacme*, *Schlechterella*, and *Camptocarpus* are coded as possessing gynostegial coronas composed of free staminal segments, as observed by Nilsson et al. (1993) in *Raphionacme*.

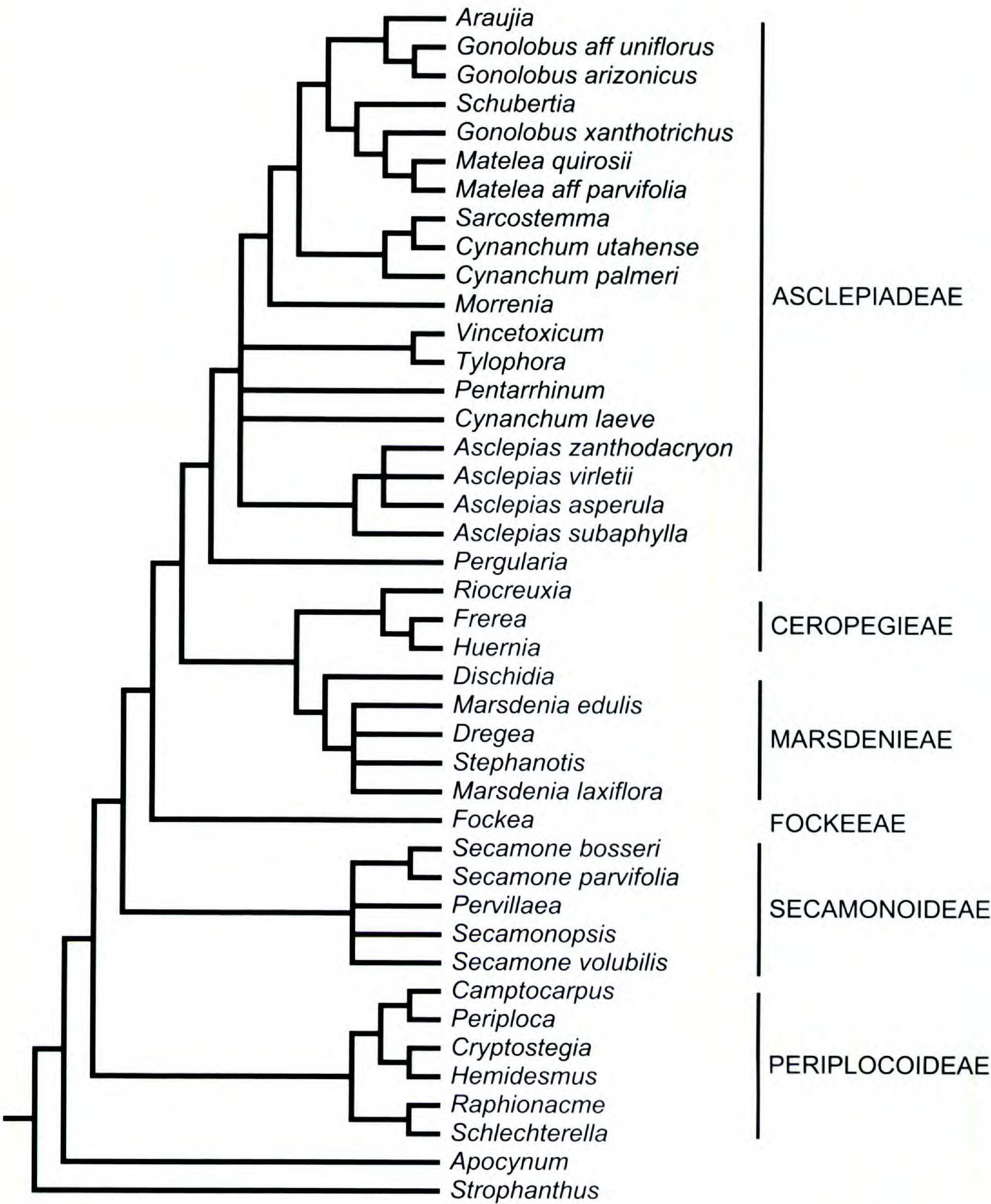


Figure 1. Phylogenetic hypothesis of broad-scale relationships in Asclepiadaceae based on maximum parsimony analysis of partial and complete *matK* sequences (L. Civeyrel & M. Fishbein, unpublished; cf. Civeyrel et al., 1998). Subfamilial and tribal membership is indicated for groups supported as clades. Asclepiadoideae, consisting of Asclepiadeae, Ceropegieae, Marsdenieae, and Fockeeae, are monophyletic, but are not labeled.

ideae are likely homologous; and (2) pollinia of some or all Periplocoideae *may* be homologous to those of other asclepiads; however, the imperfect understanding of the phylogeny of Periplocoideae at present prevents assessment of this hypothesis. With the limited sampling in the present study, pollinia of Periplocoideae are not reconstructed as homologous with those of other asclepiads. If current taxonomy (Venter & Verhoeven, 1997) reflects phylogenetic history, it appears that pollinia may have evolved independently on several occasions in Periplocoideae, based on the distribution of

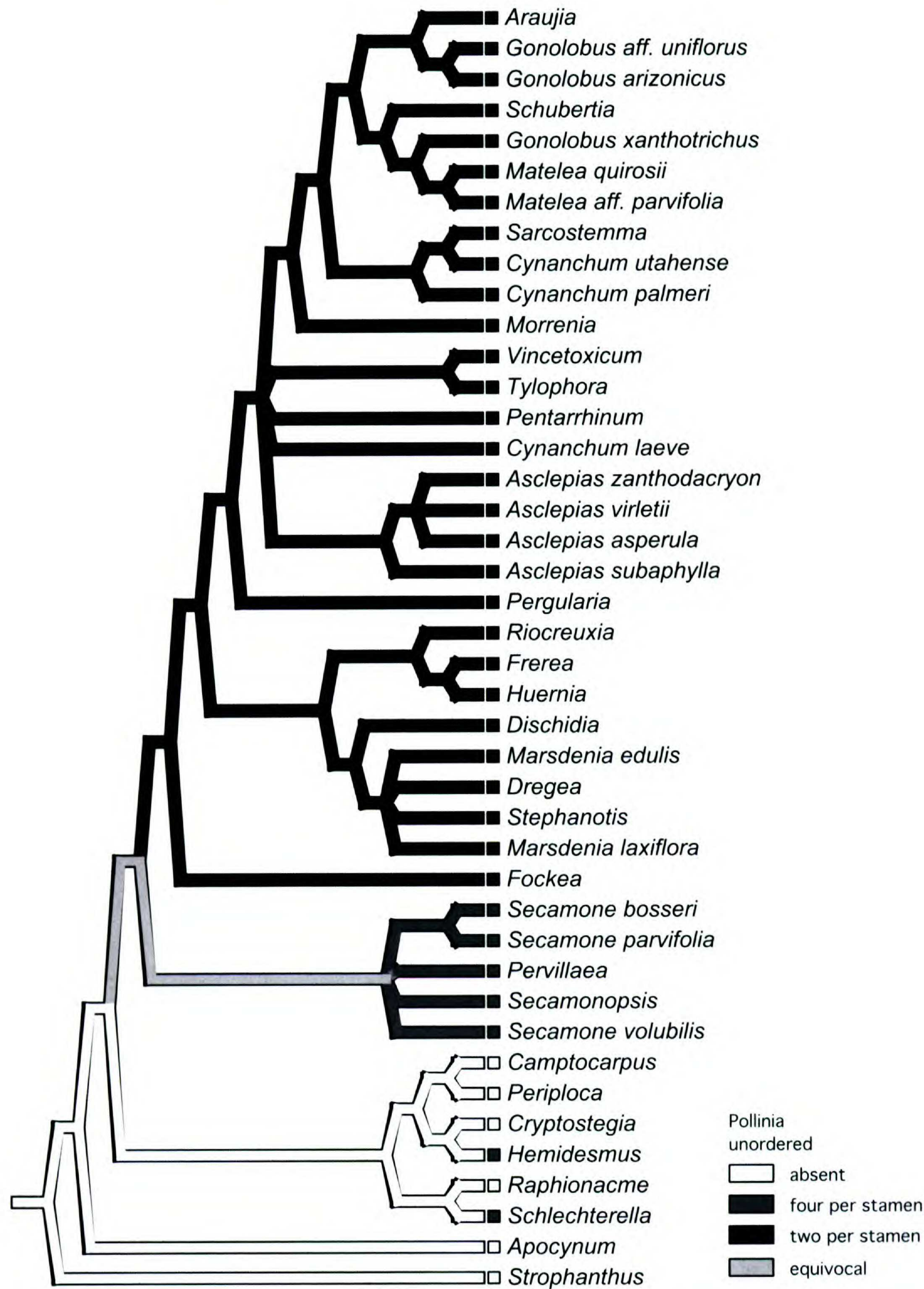


Figure 2. Maximum parsimony reconstruction of the evolutionary history of pollinia number, based on the cladogram in Figure 1. Character states are treated as unordered with equal transition probabilities among states. Ancestors and branches reconstructed as equivocal are inferred with equal parsimony to be lacking pollinia or to possess two or four pollinia per stamen. Additional reconstructions found with alternate transition probabilities are discussed in the text.

pollinia among putatively isolated genera in each of the three recognized tribes. If pollinia among most Periplocoideae are homologous, then multiple reversions to free tetrads must be inferred. The contrast between the lability of pollen aggregation in Periplocoideae and fixity in remaining asclepiads is noteworthy. Future studies evaluating the phylogenetic homology of pollinia, the number of gains (and losses?), and possible selective advantages would be of great interest.

Pollinium orientation has been used as a diagnostic character for suprageneric taxa recognized within Asclepiadoideae (e.g., Endlicher, 1838; reviewed in Rosatti, 1989; Swarupananadan, 1996; Civeyrel et al., 1998). Often, three tribes have been recognized defined by erect (Marsdenieae; note that this group has received a variety of tribal names), horizontal (Gonolobeae), and pendulous (Asclepiadeae) pollinia. Ceropegieae (Stapelieae of most modern authors, e.g., Liede & Albers, 1994), which are often recognized as an additional tribe, share erect pollinia with Marsdenieae. However, the diagnostic value of pollinia orientation was questioned due to the presence of intermediate or seemingly discordant orientations of some species, especially in Gonolobineae (Woodson, 1941; Rosatti, 1989; Kunze, 1995b; Liede, 1996; Swarupananadan et al., 1996; Civeyrel et al., 1998; Endress & Bruyns, 2000). Swarupananadan et al. (1996) re-evaluated this partitioning of pollinium orientation and presented refined categories, emphasizing the importance of the orientation of the anther locule and the position of attachment of the translator. Thus, the horizontally oriented pollinia of Gonolobae have morphologically equivalent translator attachments as the pendulous pollinia of Asclepiadeae. Swarupananadan et al. (1996) advocated using multiple criteria to evaluate whether the translator is attached to the part of the pollinium positioned apically or basally in the locule. I have adopted these criteria for analyzing the evolution of pollinium orientation, bearing in mind the exceptions noted by Endress and Bruyns (2000). Also, I have treated the very different adhesive attachment of pollinia to translators in Periplocoideae as non-homologous (see Table 3).

As with pollinia number per stamen, the evolution of the position of translator attachment is reconstructed to have been conservative (Fig. 3). Assuming that pollinia originated once in the common ancestor of Secamonoideae and Asclepiadoideae (see above), the ancestral point of attachment is unambiguously reconstructed to be basal. This orientation is retained in Secamonoideae and several lineages of Asclepiadoideae: Fockeeae, Marsden-

ieae, and Ceropegieae. A single change from basal to apical translator attachment is inferred in the ancestor of Asclepiadeae; no reversals are apparent among the representatives of this large tribe. Thus, no homoplasy is evident in the single most parsimonious reconstruction. It should be noted, however, that the sparse sampling in the present study may obscure homoplasious convergence to apical attachment among clades coded as uniformly basal or (more likely) reversal to basal attachment in Asclepiadeae (Endress & Bruyns, 2000). A rigorous basis for assessing the homology of ambiguous cases would be a comparative ontogenetic study of pollinaria (cf. Safwat, 1962; Kunze, 1993).

ORIGIN AND DIVERSIFICATION OF CORONAS

Corolline coronas. Corolline coronas are defined by structural and topological criteria: (1) they are composed of five distinct segments; and (2) they are positioned on the corolla, aligned with the sinuses of the limb (Good, 1956; Kunze, 1990; Nilsson et al., 1993). My analysis of corolline coronas explicitly excludes annular coronas (Liede & Kunze, 1993), which are conspicuous in a number of Gonolobinae and Ceropegieae, but do not appear to be homologous (see Endress & Bruyns, 2000, for a contrasting interpretation). Corolline coronas have been considered to be prevalent in Periplocoideae, but very uncommon in Asclepiadoideae (Kunze, 1990; Liede & Kunze, 1993; Nilsson et al., 1993). They have been reported from Secamonoideae, but their distribution in this subfamily has been little discussed (Safwat, 1962; Kunze, 1990). Corolline coronas are also found widely among non-asclepiad Apocynaceae (Kunze, 1990; Endress & Bruyns, 2000). The taxonomic distribution of corolline coronas has suggested that they are ancestral in Asclepiadaceae (Good, 1956; Kunze, 1990; Liede & Kunze, 1993). Although most Periplocoideae are described as having corolline coronas, some genera possess coronas that, while similar in form, appear to be more closely associated with the stamens than the corolla, e.g., *Raphionacme* Harv. (including *Schlechterella*) and *Finlaysonia* Wall. (Kunze, 1990; Nilsson et al., 1993; Forster, 1996; Venter & Verhoeven, 1997; see also Endress & Bruyns, 2000). In *Raphionacme*, ambiguity is due to the attachment of the corona segments near the point of divergence of stamens and corolla (Kunze, 1990; Nilsson et al., 1993). To account for this ambiguity, two codings of the presence of corolline coronas among Periplocoideae were explored (Tables 2, 3). In character 3a, I coded the coronas of all exemplars of Periplocoideae as being corolline, as im-

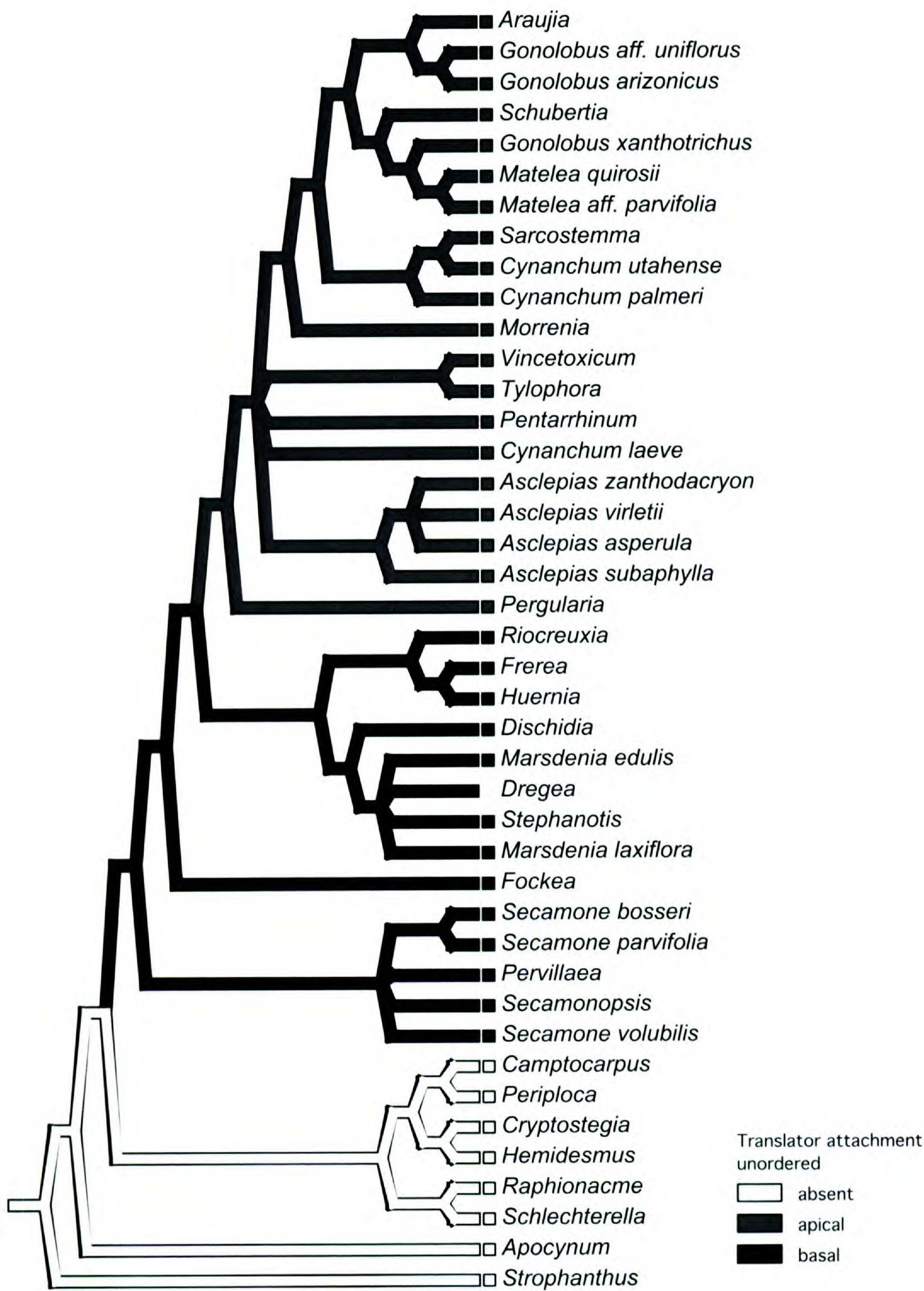


Figure 3. Maximum parsimony reconstruction of the evolutionary history of position of translator attachment to the pollinium, based on the cladogram in Figure 1. Character states are treated as unordered with equal transition probabilities among states.

plied by Kunze (1990). In character 3b, I coded all exemplars of Periplocoideae with ambiguous corona position (*Raphionacme*, *Schlechterella*, *Camptocarpus* Decne.) as lacking corolline coronas (but possessing gynostegial coronas; see below).

Parsimony reconstruction of the evolutionary history of corolline coronas, assuming their uniform presence in Periplocoideae (character 3a), requires little homoplasy (Fig. 4). The common ancestor of Asclepiadaceae is inferred to possess a corolline corona, which is a retained plesiomorphy present in related Apocynaceae (cf. Good, 1956; Kunze, 1990; Liede & Kunze, 1993). This ancestral corolline corona is retained in Periplocoideae, and no losses of corolline coronas are inferred among the sampled taxa. Loss of the corolline corona may have occurred at least once in Periplocoideae, as they have been reported to be lacking in three unsampled genera (*Baseonema* Schltr. & Rendle, *Baroniella* Costantin & Gallaud, *Phyllanthera* Blume; Venter & Verhoeven, 1997). However, Klackenberg (1997) has interpreted the corona in these genera to be a unique corolline form in which the segments occur in a novel position aligned with the corolla lobes. If interpreted correctly, such coronas would represent a distinct form not easily homologized with corolline or other gynostegial forms.

Asclepiadoideae uniformly lack corolline coronas (but see reports of secamonoid-like ridges in several genera of Marsdenieae in Hooker, 1883; Good, 1956; Kunze, 1990; Goyder, 1994; Li et al., 1995; Forster, 1996). Whether this absence is synapomorphic for Asclepiadoideae is equivocal, due to equally parsimonious reconstructions of the common ancestor of Asclepiadoideae and Secamonoideae. The ambiguity arises because of variation in the presence of corolline coronas among Secamonoideae (Safwat, 1962; Kunze, 1990; Klackenberg, 1992a, b, 1995; Li et al., 1995; Civeyrel & Klackenberg, 1996; Forster, 1996). Two of the five exemplars of this subfamily are coded as possessing corolline coronas. The phylogenetic placement of these exemplars results in an equivocal reconstruction of corolline corona presence in the common ancestor of Secamonoideae, which results in the ambiguity deeper in the phylogeny. Thus, sampling of Secamonoideae plays a crucial role in the inference of whether Secamonoideae or Asclepiadaceae + Secamonoideae ancestrally possessed a corolline corona. It is not possible at this time to predict whether more complete sampling would favor the presence or absence of corolline coronas in these ancestors. Thus, the exact point in the phylogeny where the loss of the corolline corona in Asclepiadaceae occurred cannot be determined (i.e., wheth-

er it occurred in the immediate ancestor of Asclepiadoideae or the common ancestor of Asclepiadoideae and Secamonoideae). Further, it cannot be determined whether any or all corolline coronas present in Secamonoideae are retained from the plesiomorphic presence in Periplocoideae and non-asclepiad Apocynaceae, or represent one or more instances of regaining lost coronas. A hint that corolline coronas are not homologous in Secamonoideae and Periplocoideae is that corolline coronas of Secamonoideae (and similar coronas of Asclepiadoideae) are invariably described as “pads,” “ridges,” and “cushions” (Kunze, 1990; Li et al., 1995; Forster, 1996), rather than as scales and filaments typical of Periplocoideae (Kunze, 1990; Nilsson et al., 1993; Klackenberg, 1998). Although positioned similarly, structural differences place the homology of these coronas in doubt.

Allowing for the absence of corolline coronas in some Periplocoideae (character 3b, Tables 2, 3) results in greater ambiguity in ancestral state reconstructions and a higher level of homoplasy (Fig. 5). The presence of a corolline corona in the ancestors of Asclepiadaceae, Periplocoideae, Secamonoideae, and Asclepiadoideae + Secamonoideae is equivocal in each case. This greater degree of uncertainty is due entirely to variation in the presence of corolline coronas among Periplocoideae. As a result, it is equally parsimonious to infer that those Periplocoideae with corolline coronas have retained them from non-asclepiad relatives, or that they have evolved convergently. Again, sampling may affect whether the presence of a corolline corona is most parsimoniously inferred to be plesiomorphic or convergent. Because most genera of Periplocoideae have coronas that are clearly of the corolline type (Kunze, 1990; Nilsson et al., 1993; Venter & Verhoeven, 1997), it is possible that additional sampling would favor reconstructions in which Periplocoideae retain an ancestral corolline corona. Such a scenario implies at least two independent losses of corolline coronas within Periplocoideae (Fig. 5), in addition to the putative cases discussed above.

Gynostegial coronas. Gynostegial coronas exhibit a far greater range of diversity of form than corolline coronas. My use of “gynostegial” corona follows Liede and Kunze (1993) and is largely equivalent to the “true” corona of Woodson (1941) and the “staminal” corona of Schumann (1895), Good (1956), and Kunze (1990). I coded gynostegial coronas as exhibiting two basic forms: separate staminal segments (Fig. 6) and united staminal and interstaminal segments (Fig. 7). Although Liede and Kunze (1993) distinguished staminal and interstaminal corona segments as fundamentally dis-

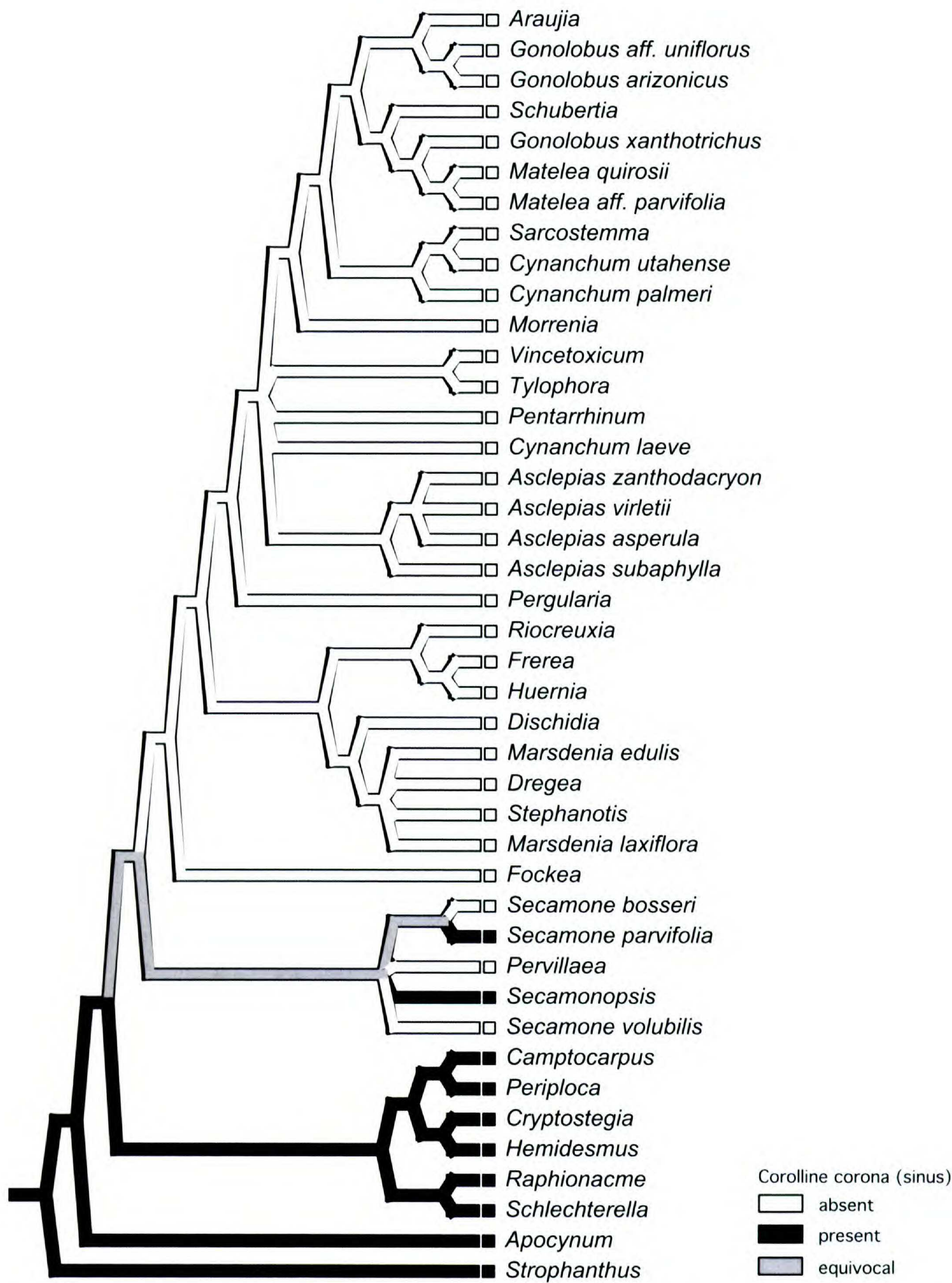


Figure 4. Maximum parsimony reconstruction of the evolutionary history of corolline coronas, based on the cladogram in Figure 1 and the coding of character 3a (Tables 2, 3).

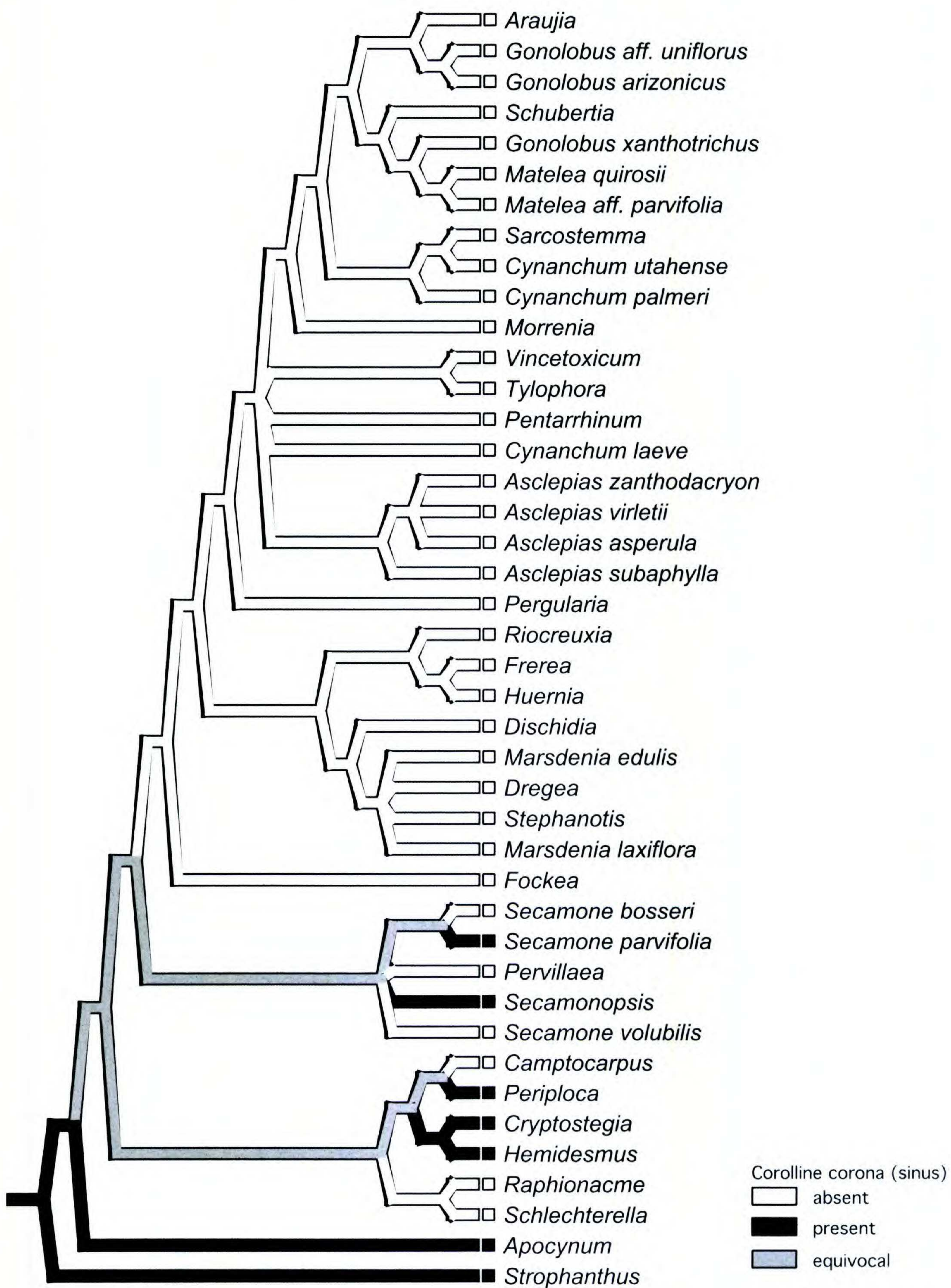
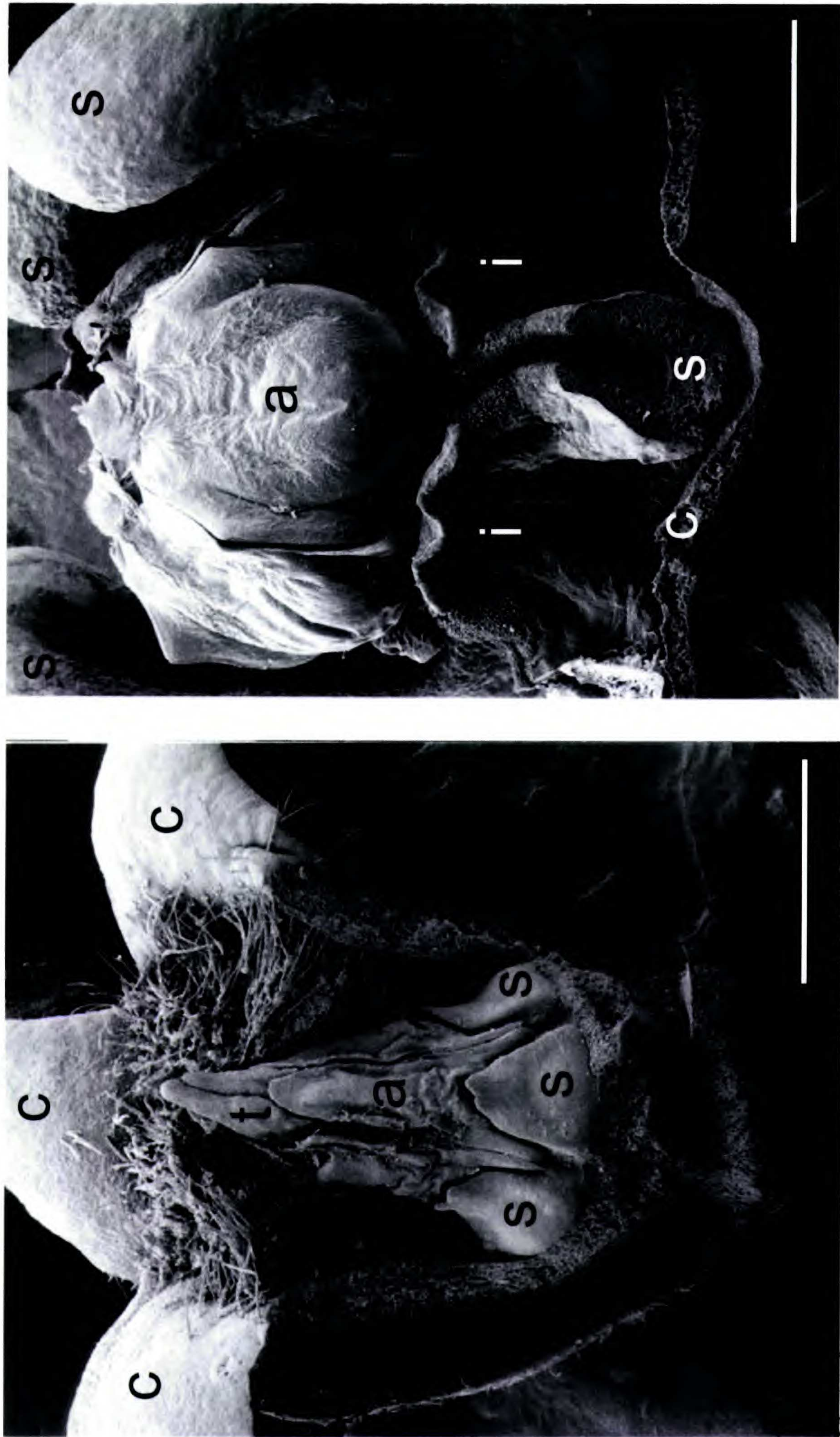


Figure 5. Maximum parsimony reconstruction of the evolutionary history of corolline coronas, based on the cladogram in Figure 1 and the coding of character 3b (Tables 2, 3).



Figures 6, 7. Scanning electron micrographs of mature flowers showing gynostegial coronas. Flowers are viewed obliquely from the side. Portions of the perianth (Figs. 6, 7) and corona segments (Fig. 7 only) were removed to reveal hidden features. Abbreviations: a = corolla, i = interstaminal segment of corona, s = staminal segment of corona, t = style apex. Methods of specimen preparation and microscopy will be presented elsewhere. —6 (left). *Marsdenia edulis* (Fishbein 3703, Sonora, Mexico, WS). The gynostegial corona is composed of free, appressed, deltoid, staminal segments. Scale bar = 1.76 mm. —7 (right). *Asclepias asperula* (material collected by M. Fishbein from the same population as *Martin s.n.*, 10 July 1968, Arizona, U.S.A., ARIZ). The gynostegial corona is composed of large, clavate, deeply grooved, staminal segments united with small interstaminal segments that appear as “m”-shaped platforms. Scale bar = 1.76 mm.

tinct types (i.e., as different from one another as each is from corolline coronas), there are three reasons to prefer treating these types as homologous, differing simply through elaboration in adjacent sectors of the flower. First, interstaminal segments are almost always united with staminal segments (Liede & Kunze, 1993). Second, there are many taxa (e.g., *Cynanchum* L.; Liede & Kunze, 1993; Endress & Bruyns, 2000) in which the corona is tubular, with little elaboration in the staminal or interstaminal sectors. Third, coronas with interstaminal segments, but lacking staminal segments, never occur (Liede & Kunze, 1993). Rather than suggesting that there are two distinct gynostegial corona types, the distribution of corona forms (Kunze, 1990, 1995b, 1997; Liede & Kunze, 1993) implies that homologous gynostegial coronas simply vary in the degree to which elaboration is manifest in the interstaminal sector. The only ontogenetic data bearing on this question (Endress & Bruyns, 2000) are consistent with the interpretation adopted here. Regardless of how these coronas are allocated into types, the evolutionary analysis presented here allows for explicit evaluation of the homology of interstaminal and staminal coronas and the pattern of their diversification.

As with the analysis of corolline coronas, reconstruction of the evolutionary history of gynostegial coronas depends on the assessment of the corona type of Periplocoideae. I begin by assuming that all coronas of Periplocoideae are corolline, as in character 3a, and that gynostegial coronas are absent (character 4a, Tables 2, 3). Under this scenario, the common ancestor of Asclepiadaceae is inferred unambiguously to lack a gynostegial corona (Fig. 8). The time of origin of the gynostegial corona, however, is ambiguous. Asclepiadoideae are inferred to possess a gynostegial corona ancestrally, but the presence of this corona type in the common ancestor of Asclepiadoideae and Secamonoideae is equivocal. It is equally parsimonious to infer that this ancestor lacked a gynostegial corona, possessed a corona of distinct staminal segments, or possessed a corona of united staminal and interstaminal segments. This ambiguity arises because the lineages descending from this ancestor are inferred to have evolved different gynostegial corona types: the ancestral corona type of Asclepiadoideae is composed of staminal and interstaminal segments, but that of Secamonoideae is composed only of staminal segments (Fig. 8). Any step matrix that weights the gain of gynostegial coronas greater (no matter how slightly) than transitions between distinct staminal coronas and united staminal and interstaminal coronas would make the inference of a

lack of gynostegial corona in the common ancestor of Asclepiadoideae + Secamonoideae less parsimonious than the presence of either type of gynostegial corona. Thus, weighting the origin of the gynostegial corona greater than transitions between free staminal and united staminal and interstaminal forms supports the single origin of gynostegial coronas in the common ancestor of Asclepiadoideae and Secamonoideae, although the form of the corona is equivocal.

Coronas of united staminal and interstaminal segments are restricted to Asclepiadoideae, and are inferred to be the ancestral corona form in the subfamily (Fig. 8). Although the reduction to two anther locules has long been noted as a synapomorphy of this subfamily (see above), the importance of the form of the gynostegial corona has been less appreciated. Within Asclepiadoideae, there is a low level of homoplasy in gynostegial coronas, among sampled taxa. Most importantly, the tribe Marsdenieae is characterized by a corona composed of distinct staminal segments (Fig. 6). Although this corona type is shared with Secamonoideae, the most parsimonious inference is that it is convergent in these clades, rather than phylogenetically homologous. Thus, a gynostegial corona of distinct staminal segments appears as a synapomorphy of Marsdenieae. It is noteworthy that Swarupanandan et al. (1996) could find no morphological synapomorphy for Marsdenieae, which they submerged under Stapelieae (= Ceropegieae). Convergence of staminal coronas in Marsdenieae and Secamonoideae also refutes Kunze's (1995a) hypothesis that staminal coronas are homologous and plesiomorphic in these groups.

Two instances of homoplasy are indicated in the tribe Asclepiadeae, among sampled taxa. *Cynanchum laeve* (Michx.) Pers. possesses a corona of distinct staminal segments, which must be regarded as convergent with those of Marsdenieae and Secamonoideae. Such coronas are not uncommon among members of subtribe Metastelminae (e.g., *Metastelma* R. Br.). At this time, it is unclear how many such instances of convergence will be demonstrated in Asclepiadeae, because of the limited sampling in the present study. *Cynanchum utahense* (Engelm.) Woodson lacks a corona entirely; this is clearly a reversal to the absence of a gynostegial corona found in Periplocoideae and non-asclepiad Apocynaceae. Other instances of the absence of a gynostegial corona are well known in Asclepiadeae, especially in subtribe Astephaninae (e.g., *Astephanus* R. Br.).

Recoding some Periplocoideae as possessing a gynostegial corona (character 4b, Tables 2, 3) re-

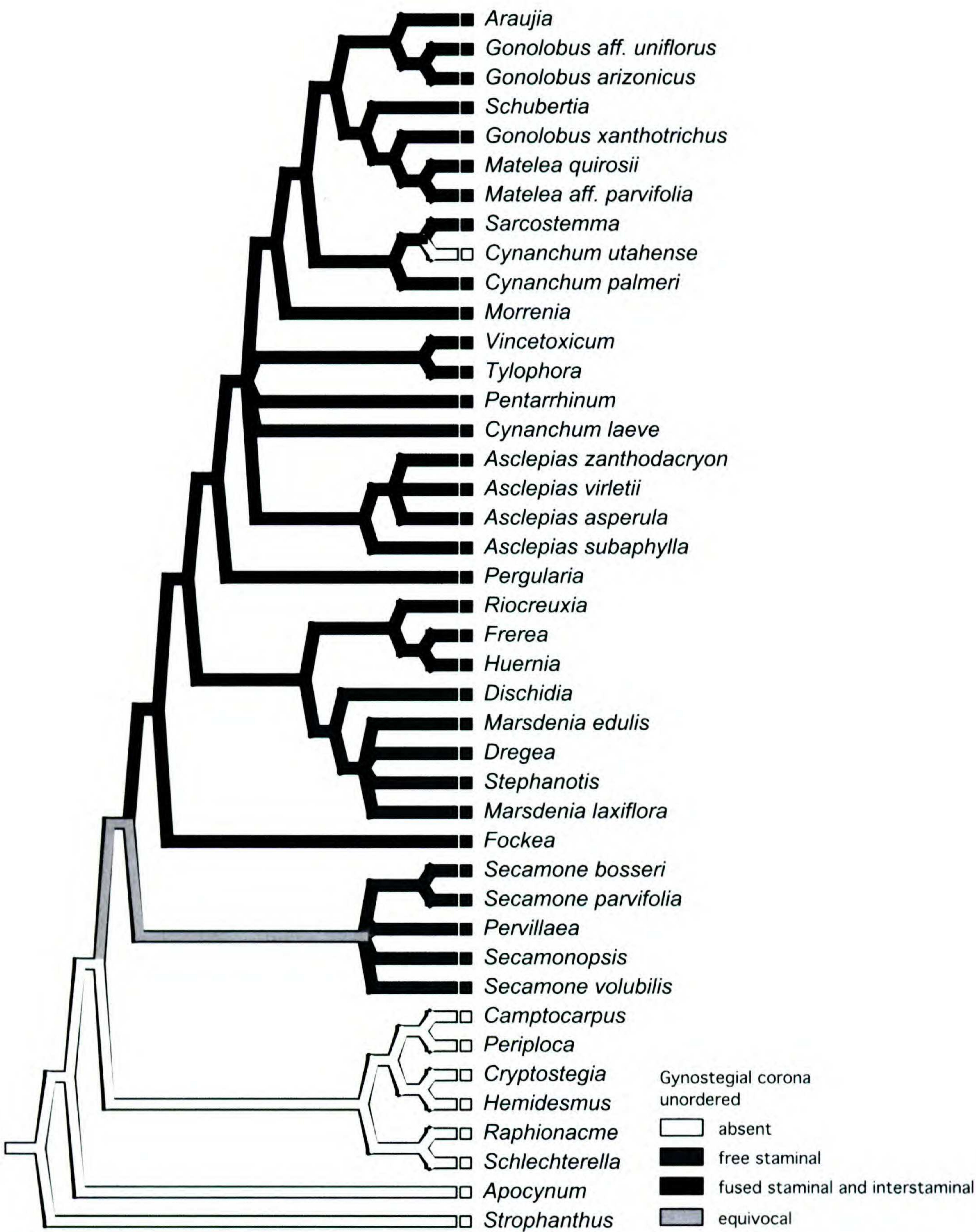


Figure 8. Maximum parsimony reconstruction of the evolutionary history of gynostegial coronas, based on the cladogram in Figure 1 and the coding of character 4a (Tables 2, 3). Character states are treated as unordered with equal transition probabilities among states. The ancestor of and branch leading to Secamonoideae + Asclepiadoideae is reconstructed with equal parsimony to be lacking a gynostegial corona, possessing a corona of free staminal segments, or possessing a corona of united staminal and interstaminal segments. The ancestor of and branch leading to Secamonoideae is reconstructed as equivocal because of the polytomy present in the strict consensus of most-parsimonious trees (MPTs). All resolutions of secamonoid phylogeny present in the MPTs result in reconstruction of the ancestor as possessing a corona of free staminal segments. Additional reconstructions found with alternate transition probabilities are discussed in the text.

sults in ambiguity concerning the ancestral absence of a gynostegial corona in Asclepiadaceae, and introduces additional homoplasy among Periplocoideae (Fig. 9). The presence of gynostegial coronas in some Periplocoideae permits with equal parsimony the common ancestor of Asclepiadaceae to either lack a gynostegial corona or possess one of distinct staminal segments; a corona of united staminal and interstaminal segments, however, is less parsimonious. Similarly, it is equally parsimonious to infer that the ancestor of Periplocoideae lacked a gynostegial corona or possessed one of distinct staminal segments. If such a corona was absent in the ancestor of Periplocoideae, then independent derivation is implied within the subfamily (Fig. 9). If a gynostegial corona was ancestral in Periplocoideae, then one or more losses must have occurred. Because taxa bearing ambiguous corona types may be oversampled in this study (see above), further sampling of Periplocoideae may support the convergent evolution of gynostegial coronas in this subfamily, if they indeed should be coded as gynostegial (Kunze, 1990; Nilsson et al., 1993; Endress & Bruyns, 2000).

PHYLOGENETIC SENSITIVITY

The evolutionary scenarios inferred here from maximum parsimony reconstructions are specific to the preliminary phylogeny derived from analysis of partial *matK* sequences (L. Civeyrel & M. Fishbein, unpublished data). Errors in the estimation of phylogeny may lead to errors in estimates of timing, location, and degree of homoplasy in character evolution (see Ackerly & Donoghue, 1998, for a robust analysis of phylogenetic sensitivity). An analysis of *rbcL* sequence data suggested that Asclepiadaceae as circumscribed here are polyphyletic (Sennblad & Bremer, 1996). Although support for the polyphyly of Asclepiadaceae found with *rbcL* sequences (Sennblad & Bremer, 1996) was much weaker than support for the monophyly of Asclepiadaceae found with *matK* (Civeyrel et al., 1998; L. Civeyrel & M. Fishbein, unpublished data), sampling is poor in both data sets and alternate topologies should be considered. A recent study employing a different, non-coding region of chloroplast DNA and broader sampling reported non-monophyly of Asclepiadaceae (Potgieter & Albert, 2001). Thus, I have evaluated most parsimonious reconstructions of the evolution of pollinia and corona characters assuming a closer relationship of Periplocoideae to non-asclepiad Apocynaceae than to the remainder of Asclepiadaceae (Sennblad & Bremer, 1996; Potgieter & Albert, 2001).

The evolutionary reconstructions based on the *matK* phylogeny are robust to the non-monophyly of Asclepiadaceae. For both pollinia characters, the phylogenetic placement of character transformations is identical for topologies in which Asclepiadaceae are monophyletic or polyphyletic. Because Periplocoideae retain ancestral characteristics of non-asclepiad Apocynaceae, placement of Periplocoideae as sister to these lineages does not alter inferences about character evolution. However, the phylogenetic relationships among unsampled Periplocoideae are unknown, and could support an earlier origin of pollinia in the common ancestor of Asclepiadaceae, if asclepiads are monophyletic. Hypotheses of the pattern of corona evolution are also insensitive to phylogenetic uncertainty, *if* periplocoid coronas are assumed to be uniformly corolline (characters 3a, 4a). However, polyphyly of Asclepiadaceae does affect reconstructions of corona evolution when gynostegial coronas are coded as occurring in some Periplocoideae (characters 3b, 4b). Under this scenario, polyphyly of Asclepiadaceae has no effect on the inference of character evolution in Secamonoideae and Asclepiadoideae. Periplocoideae, however, are unambiguously inferred to ancestrally possess a corolline corona, as in reconstructions of character 3a. As a result, the gynostegial coronas of Periplocoideae are unambiguously inferred to represent convergence with coronas of Asclepiadoideae and Secamonoideae. Thus, polyphyly of Asclepiadaceae does not introduce new hypotheses of character evolution; it merely limits the parsimonious reconstructions of corona evolution under a single scenario, in which some periplocoid coronas are interpreted to be gynostegial.

CONCLUSIONS

The exquisitely complex flowers of Asclepiadaceae are tempting subjects for the study of innovation and diversification. Complexity is due in part to the unusually high degree of structural and functional synorganization between the androecium and gynoecium, as exemplified by the pollinarium. Complexity is due also to elaborate diversification of the corona. Pollinaria and coronas are distinctive features of Asclepiadaceae that potentially represent innovations integral to the radiation of this clade. The phylogenetically explicit approach adopted in this paper provides a preliminary analysis of the timing and patterns of diversification of these structures, as well as an assessment of the level of homoplasy. Although homology assessments and evolutionary reconstructions for these struc-

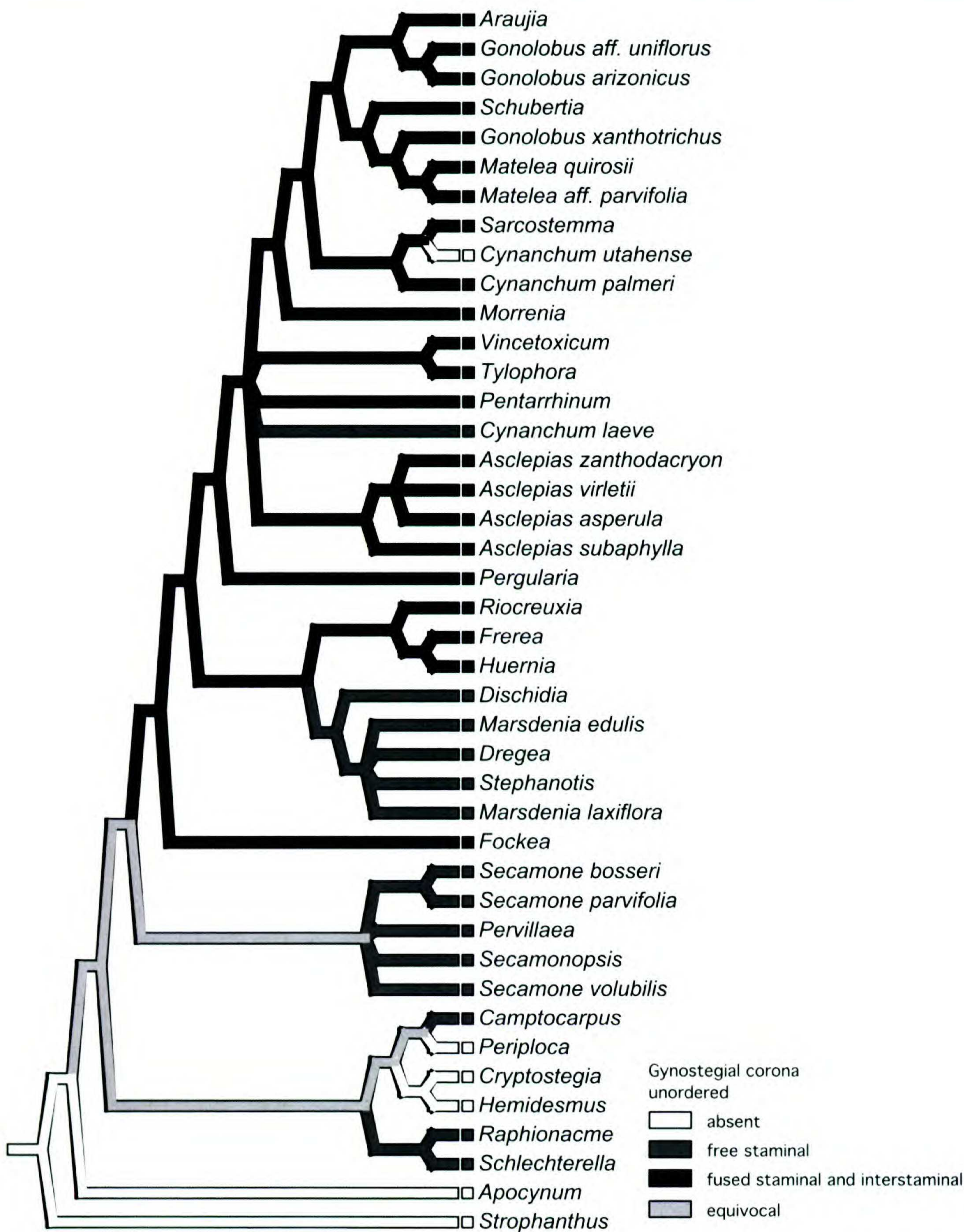


Figure 9. Maximum parsimony reconstruction of the evolutionary history of gynostegial coronas, based on the cladogram in Figure 1 and the coding of character 4b (Tables 2, 3). Character states are treated as unordered with equal transition probabilities among states. The ancestor of and branch leading to Secamonoideae + Asclepiadoideae is reconstructed with equal parsimony to be lacking a gynostegial corona, possessing a corona of free staminal segments, or possessing a corona of united staminal and interstaminal segments. The ancestor of and branch leading to Secamonoideae is reconstructed as equivocal because of the polytomy present in the strict consensus of most-parsimonious trees (MPTs). All resolutions of secamonoid phylogeny present in the MPTs result in reconstruction of the ancestor as possessing a corona of free staminal segments. The ancestor of and branch leading to Asclepiadaceae is reconstructed with equal parsimony to be lacking a gynostegial corona or possessing a corona of free staminal segments; a corona of united staminal and interstaminal segments is less parsimonious.

tures have been presented in the past, rigor has been limited by the lack of an explicit phylogenetic hypothesis (Woodson, 1941; Good, 1956; Kunze, 1990, 1995a; Liede & Kunze, 1993; Swarupandan et al., 1996; Endress & Bruyns, 2000) or minimal taxon sampling and attention to topological ambiguity and homology decisions (Wanntorp, 1988; Judd et al., 1994). Admittedly, taxon sampling in the present study is still inadequate to fully explore the range of corona evolution of Asclepiadaceae and the origin of pollinia in Periplocoideae, subjects still ripe for further investigation.

Pollinaria and coronas exhibit contrasting evolutionary patterns. The pollinarium is a novel feature of Asclepiadaceae that has undergone relatively conservative evolution with comparatively little diversification. Reconstructions of the evolutionary history of pollinium number per flower and position of translator attachment show little homoplasy. Shifts in the number and orientation of pollinia correspond to the origin of major clades, as largely reflected in classifications of the family (Brown, 1811; Endlicher, 1838; Decaisne, 1844; Schumann, 1895; Liede & Albers, 1994; Liede, 1997; Endress & Bruyns, 2000). Once such changes evolved, no reversals or losses are inferred to have occurred, except for Periplocoideae. Pollinia in this subfamily exhibit additional diversity in the morphology of the constituent pollen grains (Verhoeven & Venter, 2001). More thorough sampling of Periplocoideae in phylogenetic studies is necessary to evaluate the level of convergence and reversal in the evolution of pollinia. Comparative studies that contrast the conservative evolution of pollinia in Secamonoideae and Asclepiadoideae with the greater lability in Periplocoideae may be useful in evaluating Riedl's (1978) concept of evolutionary burden (see also Donoghue, 1989) as it applies to asclepiad flowers.

A further caveat pertains to the scale at which pollinarium evolution is studied. I have discussed the difficulties encountered in prior attempts to describe pollinium orientation (Woodson, 1941; Rosatti, 1989; Kunze, 1995b; Liede, 1996; Swarupandan et al., 1996; Civeyrel et al., 1998). By adopting homology criteria that are more easily assessed across Asclepiadaceae (Swarupandan et al., 1996), I have incompletely addressed the extensive variation that led to difficulties in homology assessment in the past. Careful study of variation in pollinium shape and anther orientation in a phylogenetic framework, including much more thorough taxon sampling, is required to assess the lability of pollinarium characteristics not studied in the present investigation.

The evolution of coronas appears to exhibit greater diversification with more extensive homoplasy than that of pollinaria. The presence of corolline coronas is variable in Secamonoideae and, perhaps, Periplocoideae. This variability requires that convergence and/or losses have occurred in the history of corolline coronas. Similarly, evolutionary reconstructions of the presence and form of gynostegial coronas require considerable homoplasy. The inference of evolutionary lability depends largely on homology assessment. Under some scenarios, the origin of subfamilies and tribes may be marked by large changes in corona morphology with no subsequent homoplasy (e.g., the synapomorphic loss of corolline coronas in Asclepiadoideae). In other cases, homoplasy is inferred regardless of homology assessment, as in the convergence and loss of gynostegial coronas of Asclepiadaceae. The greater degree of homoplasy in coronas than pollinaria invites inquiry into adaptive explanations. One could speculate that the greater functional diversity of coronas plays an important role. The sole function of pollinaria is the transfer of male gametes. Coronas may participate in the attraction, reward, and positioning of pollinators (Wanntorp, 1974; Kunze, 1991, 1997; Endress, 1994).

Unlike pollinaria, corolline coronas of Asclepiadaceae appear to be plesiomorphic features present in related non-asclepiad Apocynaceae. However, gynostegial coronas are potentially a novel structure of Asclepiadaceae. Gynostegial coronas appear to adopt a novel position in the flower. Different evolutionary scenarios have been proposed (cf. Kunze, 1990), under which (1) gynostegial coronas are a structure *sui generis* of Asclepiadaceae and are not homologous with corolline coronas, or (2) gynostegial coronas are derived from corolline coronas. Evidence for both hypotheses was presented by Kunze (1990), who concluded that gynostegial coronas were non-homologous with corolline coronas. Liede and Kunze (1993) indicated homology among all corona types in a linear transformation series, but also stated that some corona types are not homologous. Circumstantial support for the second scenario comes from the rarity of instances in which corolline coronas and gynostegial coronas are present in the same flower (cf. Figs. 4, 5, 8, 9), although Secamonoideae provide important exceptions (Good, 1956; Safwat, 1962; Kunze, 1990; Klackenberg, 1995; Li et al., 1995; Forster, 1996). Kunze (1990) noted the presence across Asclepiadaceae of a basal synorganized zone during flower development. Endress and Bruyns (2000) proposed the homology of this zone across Asclepiadaceae, interpreting the zone as neither corolline nor sta-

minal and suggesting that at least some corolline and gynostegial coronas may develop from this region of zonal growth. Like homology assessment of corolline and gynostegial coronas, accurate evaluation of the novelty of the gynostegial corona requires ontogenetic study in a phylogenetic framework (Hufford, 1995, 1996a, b). The importance of ontogenetic studies as a basis for homology assessment (see Kaplan, 1984) was recognized in Kunze's (1990) assessment of corona evolution and in the work of Endress and Bruyns (2000). In addition, phylogenetic analysis permits evaluation of phylogenetic homology, assessment of homoplasy, and inference of ontogenetic transformations (Hufford, 1995, 1996a, b). These analytical properties provide the strongest basis for assessing the patterns and mechanisms of morphological evolution and should guide future studies of innovation and diversification of asclepiad flowers.

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A KARYOLOGICAL SURVEY OF ASCLEPIADOIDEAE, PERIPLOCOIDEAE, AND SECAMONOIDEAE, AND EVOLUTIONARY CONSIDERATIONS WITHIN APOCYNACEAE S.L.¹

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ABSTRACT

The chromosome numbers of 672 species out of 740 taxa of the Apocynaceae in the subfamilies Asclepiadoideae, Periplocoideae, and Secamonoideae were either determined or extracted from the literature. The chromosome numbers of 299 taxa are published here for the first time, and a further 139 new counts confirm or complete previously published chromosome numbers. The basic chromosome number $x = 11$ is found to be predominant, occurring in ca. 96% of the taxa investigated. Deviations from $x = 11$ are absent in Periplocoideae and Secamonoideae, but some variation is present in Asclepiadoideae. A reduction of the karyotype to $x = 10$ is known only in the advanced tribe Asclepiadeae, where it is important in the Old World subtribe Astephaninae (*Microlooma*), as well as in the New World subtribes Metastelminae (*Funastrum*, *Orthosia*, *Philibertia*, and *Grisebachiella*) and Oxypetalinae (*Araujia* and *Tweedia*). An increase ($x = 12, 13, 14$) was found only rarely and sporadically in the subfamily Asclepiadoideae. About 6% of the species (7% of the taxa) investigated are found to be polyploid. The majority of such taxa are tetraploid with $2n = 44$; only a few are hexaploid or higher. The data on chromosome number and size presented in this paper are interpreted in relation to the systematic position and geographical distribution of the taxa investigated. On the average karyotype size diminishes from rather large chromosomes in the Periplocoideae to the smallest karyotype length in the presumed most advanced tribe of the Asclepiadoideae, the Asclepiadeae. Reduction in the basic chromosome number is regarded as only a rather recent step in genome evolution within Asclepiadeae, which has been taken place in parallel in the Old and New Worlds. Finally, comparison with data available for the Apocynaceae s. str. (Apocynoideae and Rauvolfioideae) is presented.

Key words: Apocynaceae, Asclepiadoideae, chromosome number, chromosome size, evolution, Periplocoideae, polyploidy, Secamonoideae.

According to the most recent classification, the Apocynaceae comprise the subfamilies Apocynoideae, Rauvolfioideae, Periplocoideae, Secamonoideae, and the Asclepiadoideae (Endress & Bruyns, 2000). Of these, the Periplocoideae (cf. Schlechter, 1905; Venter, 1997) and the Asclepiadoideae (Brown, 1810; Bruyns & Forster, 1991) have often been treated as separate families Periplocaceae Schltr. and Asclepiadaceae R. Br. in the past. However, present molecular data support earlier morphological insights that the most natural classification is to treat the group as a single family, and that the subfamily Asclepiadoideae is the most

highly evolved group being nested within Apocynaceae s. str., and thus must be included in Apocynaceae for the family to be monophyletic (Olmstead et al., 1993; Sennblad & Bremer, 1996). Approximately 400 genera of Apocynaceae contain about 4300 species. All subfamilies except the small Secamonoideae (9 genera, ca. 170 species; Klackenberg, in press) have been split into tribes and subtribes established mainly on morphological reasoning. Periplocoideae, which is characterized by several monotypic genera, comprises only ca. 180 species distributed among 31 genera (Venter & Verhoeven, 1997, 2001 this volume). Asclepia-

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